

Report

Visual Sensitivity Underlying Changes in Visual Consciousness

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Summary

When viewing a different stimulus with each eye, we experience the remarkable phenomenon of binocular rivalry: alternations in consciousness between the stimuli [1, 2]. According to a popular theory first proposed in 1901, neurons encoding the two stimuli engage in reciprocal inhibition [3–8] so that those processing one stimulus inhibit those processing the other, yielding consciousness of one dominant stimulus at any moment and suppressing the other. Also according to the theory, neurons encoding the dominant stimulus adapt, weakening their activity and the inhibition they can exert, whereas neurons encoding the suppressed stimulus recover from adaptation until the balance of activity reverses, triggering an alternation in consciousness. Despite its popularity, this theory has one glaring inconsistency with data: during an episode of suppression, visual sensitivity to brief probe stimuli in the dominant eye should decrease over time and should increase in the suppressed eye, yet sensitivity appears to be constant [9, 10]. Using more appropriate probe stimuli (experiment 1) in conjunction with a new method (experiment 2), we found that sensitivities in dominance and suppression do show the predicted complementary changes.

Results

The previous studies that failed to find changes in sensitivity during an episode of suppression suffered two limitations. First, the probe stimuli used to test sensitivity were very different from the stimuli engaged in rivalry. Fox and Check [9] used gratings as rival stimuli and briefly flashed monocular letters as probes, measuring letter identification performance.

Norman et al. [10] also used gratings as rival stimuli and very small monocular spots of light as probes, measuring luminance detection thresholds. In both cases, the probes had very different spatial frequency and orientation content from the rival stimuli. Because there is good evidence that adaptation is specific to the spatial properties of the adapting stimulus [11], such probes are unsuitable to quantify the supposed changing state of adaptation of the units responding to the rival stimuli. We addressed this limitation in experiment 1.

Second, the previous studies examined only the first half of a suppression episode. It is possible that the effects of adaptation reveal themselves only late in an episode of suppression. In experiment 2, we introduce a new method that allows us to study all of a suppression episode.

Experiment 1

We measured thresholds for detecting a brief increment in the contrast of either the upper or lower half of the rival target itself [12] (Figure 1). This increment was presented either early (200 ms) or late (the median of each observer's dominance durations) after onset of an episode of dominance or suppression. By pressing one of two keys, observers judged whether the probe increment was in the upper or lower half; over trials, the size of the contrast increment was adjusted using a staircase procedure to find the threshold.

Figure 2 summarizes mean probe thresholds for each observer and condition. Note that thresholds are low when sensitivity is high and vice versa. Plotted in each panel is the average increment threshold for each of the four probe conditions (early and late probes delivered during dominance and during suppression). There is considerable variability among observers in the values of these thresholds, but this could be because different observers were purposefully tested using different background grating contrasts (to slow their rivalry state durations). Observer R.B. was tested both at Vanderbilt University and at the University of Sydney, and his results measured at those two sites are comparable. R.B.'s two data sets, although shown separately in Figure 2, were averaged and treated as one observer for statistical analyses.

All observers had lower thresholds under dominance than under suppression, replicating the well-established loss in visual sensitivity that accompanies suppression phases of rivalry [13]. The magnitude of this suppression effect ranges from 0.11 to 0.52 (mean = 0.20; standard error = 0.03), which is within the range reported in many previous reports.

The plots of individual data in Figure 2 show that every observer's thresholds rose during dominance from early to late. This is significant overall (one-tailed $t(5) = 2.85$, $p < 0.05$). Although some observers' thresholds fell during suppression from early to late, others' thresholds did not. Overall, there was no significant change over time in suppression thresholds ($t(5) = 0.32$, $p > 0.05$). When the dominance and suppression thresholds are combined into suppression depth (the ratio of dominance to suppression thresholds), as is typical [14, 15], there is a significant reduction of suppression depth between early and late probes (one-tailed $t(5) = 2.32$, $p < 0.05$). This result differs from those of earlier studies that found no change in suppression depth over time [9, 10], supporting

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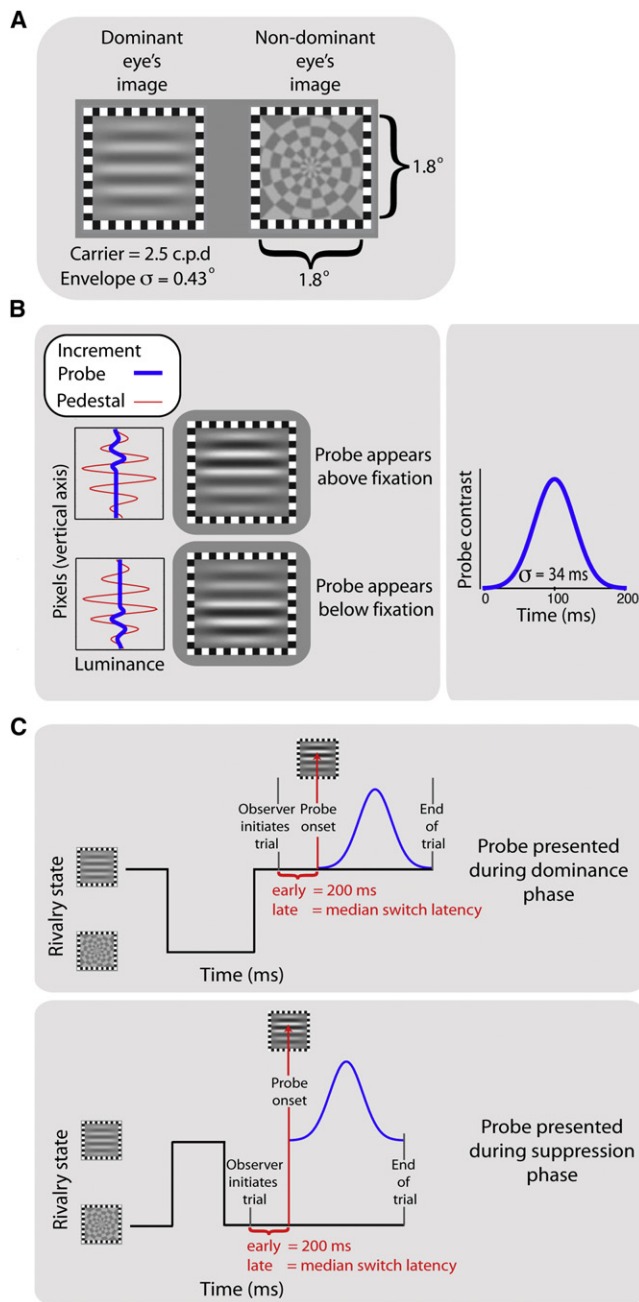


Figure 1. Methods for Experiments 1 and 2

(A) Illustrations of the rival targets used in experiments 1 and 2. The observer's rivalry-dominant eye always received the grating. (B) The two panels on the left plot the luminance profiles of the grating (red; pedestal) and the probe (blue). The probes were contrast increments added to the upper or lower half of the grating (illustrated on the right), with the magnitude of the contrast increment varied adaptively to find the contrast increment threshold. The probe contrast increment was added smoothly over time with a Gaussian profile (plot on right). (C) In experiment 1, a series of short trials was used. Observers waited for rivalry to stabilize, then pressed a key to show the probe once the desired state was achieved (dominance or suppression, depending on condition). A brief period elapsed, either 200 ms for early probes or the median dominance duration for late probes (approximately 3 s), after which the probe contrast increment was presented. The trial terminated after the probe and the screen went blank. When the rivalry state changed prior to the onset of the probe, observers released the key, leading to the trial's being aborted.

our contention that those earlier studies used inappropriate probe stimuli. Nevertheless, the change in suppression that we found is rather small.

At least three factors may have worked against finding clearer evidence of weakening suppression over time in this study and in previous studies. First, on any particular trial in the late-probe condition, observers had to abort about 50% of trials because the rivalry state spontaneously changed before the probe could be presented (see Figure S3A available online). This made the experiment very long and tiring, preventing us from measuring potentially stronger adaptation-related changes occurring at later times.

Second, some observers may unwittingly have tried to use attention to keep rivalry in a desired state until the probe was presented. This would be undesirable, because attention can alter rivalry dynamics [16, 17].

Third, the option to abort trials when the rivalry state appeared to change prior to probe presentation led to an unexpected criterion problem in that observers were more likely to abort suppression trials than dominance trials (Figure S3B). This probably resulted from observers' applying a strict criterion to ensure that no trace of the suppressed grating was visible during suppression trials (as instructed). Consequently, some legitimate trials in which the probe was visible may have been interpreted as a break in suppression just prior to the probe and were therefore aborted. This would tend to raise thresholds, counteracting the expected lowering of suppression thresholds as a result of recovery from adaptation.

What is needed is a new approach to avoid these problems; we developed one for experiment 2.

Experiment 2

With our new method, observers continuously tracked their experience of rivalry over 3 min trials by pressing one of two keys for exclusive visibility of one or the other rival stimuli, and they also responded to fixed-contrast probes presented intermittently every few seconds (Figure 3A), marked by a brief tone, by pressing one of two other keys for upper or lower increments. Probe increment contrast was optimized for each observer as the mean of thresholds for dominance and suppression.

Because of response latency, the reported state changes during rivalry tracking necessarily lagged the perceived rivalry changes by between 400 and 500 ms. To correct for this, we advanced the key tracking records of all observers by 450 ms.

Figure 4A shows probe performance, as points and lines, plotted against the left-hand y axis as a function of absolute time (time elapsed since onset of rivalry state). As expected, detection performance for dominance begins well above 75% correct, and performance for suppression begins below 75%. In the last time bin, performance reverses, but it is clear from the size of the associated error bars and the small number of observations per bin (plotted as gray bars against the right-hand y axis) that these performance estimates are not reliable.

Each episode of suppression had a random duration [18, 19]; it is possible this is caused by random variations in the time constants of any underlying neural adaptation, with fast adaptation yielding a short episode of suppression and slow adaptation yielding a long episode. Another way to present the data is to plot probe performance as a function of the relative timing of a probe in a given rivalry state as a proportion of that state's duration (Figure 3B). As can be seen in Figure 4B, this normalization has the added benefit of equalizing the

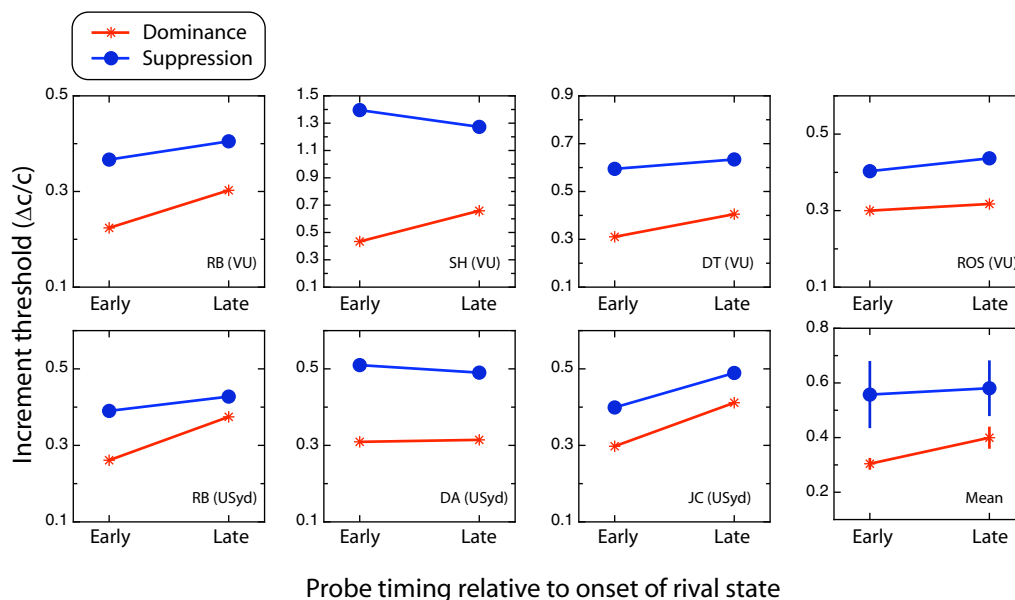


Figure 2. Results from Experiment 1

Contrast increment thresholds ($\Delta C/C$: the contrast value necessary to detect an increment divided by the contrast of the background grating, against which the increment appeared) for probe detection as a function of probe latency for dominance and suppression states. Each point is the mean of at least four staircases. Data from all six observers are shown, including R.B.'s data from two sites, together with the overall mean (bottom right) and standard errors of those means. On average, dominance thresholds are higher for late probes (i.e., sensitivity is lower), although suppression thresholds tend to remain stable.

number of observations per bin, as the gray bars show, equating statistical reliability across all bins. In the later time bins, it is clear that dominance performance declines and suppression performance improves. The performance levels are stable until after the median, illustrating the problem with the methodology of experiment 1 and of previous studies that used absolute time [9, 10]. Critically, the performance levels converge just prior to a perceptual reversal.

The complementary relationship between dominance and suppression performance is the expected signature of adaptation on reciprocal inhibition: as neurons signaling the dominant stimulus adapt over time, their ability to inhibit neurons signaling the suppressed stimulus wanes. This, then, is consistent with adaptation's playing a key role in binocular rivalry, as has long been proposed [3].

Discussion

Although other conceptualizations of rivalry have been proposed (see [Supplemental Discussion](#)), theories based on reciprocal inhibition have enjoyed enduring popularity. Adaptation is a cornerstone in most of those theories [6–8, 20]. The results obtained using our new method show for the first time the predicted reciprocal changes in suppression and dominance sensitivity during phases of rivalry that are expected on the basis of neural adaptation.

Why does this reciprocal pattern of sensitivity change emerge only when timing is expressed as a proportion of the time in a particular state of rivalry? Although the exponential decay used to describe neural adaptation is described by a time constant (implying a fixed rate), state durations during binocular rivalry alternations are close to random [21]. One possibility is that there are various sources of noise that disguise the correlation one might expect between the duration of one episode of suppression and the previous ones.

Eye blinks [22] and eye movements [23] represent possible sources of noise, and internal neural noise is another possibility [24–26]. Perhaps, too, adaptation time constants themselves are variable [27], so that adaptation rate varies over episodes of rivalry. Indeed, we demonstrate using a simple model how noisy adaptation could account for the typical positively skewed durations of rivalry states ([Figure S2](#)). In such a model, normalizing timing to the state duration would standardize all decay functions and better reveal patterns of data related to that decay. A fully developed model of bistable alternation dynamics based on the principle of noisy adaptation can be found elsewhere [28].

If adaptation is the cause of the changing sensitivity patterns over time, there is one query we must consider. Specifically, the dominance curve in [Figure 4B](#) does not conform to an exponential decline in effective contrast, as adaptation functions generally do [22]. Nor, for that matter, does the suppression curve resemble an exponential recovery function. Note, however, that growth and decay functions index adaptation's effects on contrast thresholds, whereas [Figure 4B](#) shows changes in percent-correct performance over time, measured using a fixed-contrast probe target. But our results are consistent with an exponential adaptation function if we assume that performance is governed by a compressive contrast response function, as we show in [Figure S1](#).

Although these reciprocal changes in sensitivities are consistent with adaptation and point to a causal role for adaptation in rivalry alternations, the evidence is correlational rather than definitive. It remains to be seen whether experiments in which adaption is directly manipulated will show the same relation between adaptation and sensitivity as we do in [Figure 4B](#), although we predict that they will. We know, for example, that adapting one of the rival stimuli for a second or so makes it invisible when the second rival stimulus is shown [29].

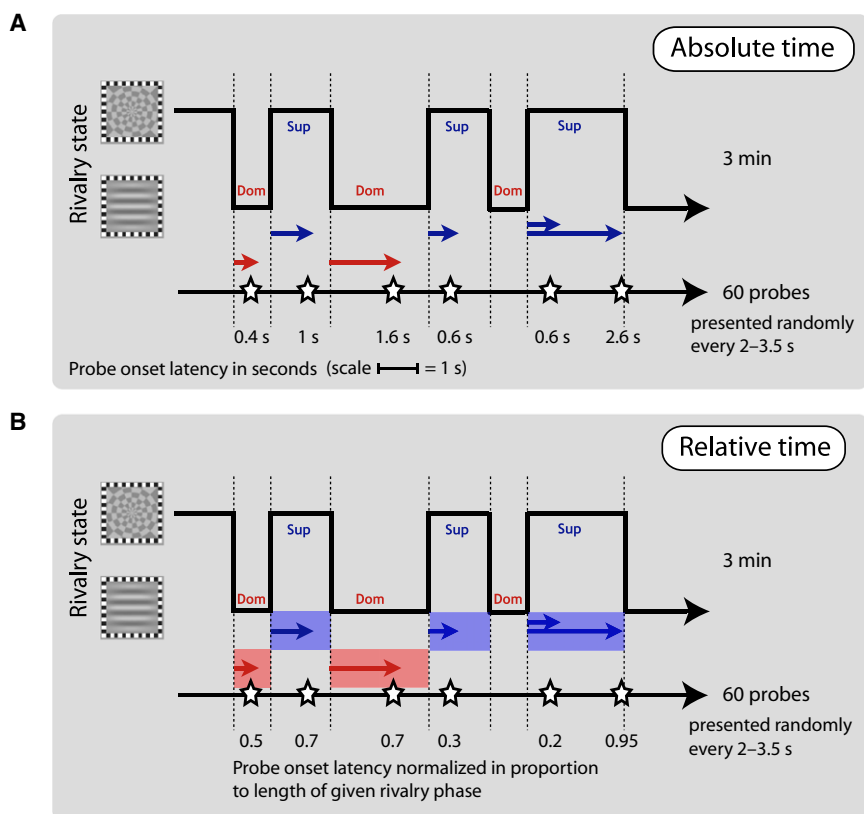


Figure 3. Methods for Experiment 2

(A and B) Observers continuously tracked their rivalry alternations in 20 trials. In each of these trials, 60 contrast-increment probes were delivered at irregular intervals to the grating viewed by one eye. We then used the tracking sequence to divide the probes into dominance and suppression phases and to determine the timing of a given probe from the onset of the current rivalry phase. Probe timing could be coded as absolute time (A) or as relative time (B).

expect to see fading of the currently dominant stimulus or some visible hints of the suppressed stimulus toward the end of an episode of dominance. Of course, at transitions between dominance of rivalry stimuli, we do briefly see combinations of the two stimuli, so-called composites [2], but we excluded these experiences from our analyses. Perhaps perceptual experience exhibits hysteresis: seeing one rival stimulus at one moment promotes seeing that same rival stimulus at the next moment despite its neurons now weakly inhibiting the neurons encoding the other stimulus. Indeed, there are examples of hysteresis effects in rivalry [30–32]. Alternatively, there may be

As a final point, we have shown that probe sensitivity changes in the way that is predicted by adaption and reciprocal inhibition theory, but this does not explain the conscious experience of rivalry: we see a dominant stimulus as dominant for all of the duration of one episode of suppression until it is replaced by the previously suppressed stimulus. One might

a separate, winner-take-all neural process determining experience. Such a process could arise at higher stages in the visual hierarchy, where competition is based on stimulus representations and not on eyes [33, 34].

In conclusion, we have used a new method that reveals clear reciprocal changes in contrast sensitivity during the course of

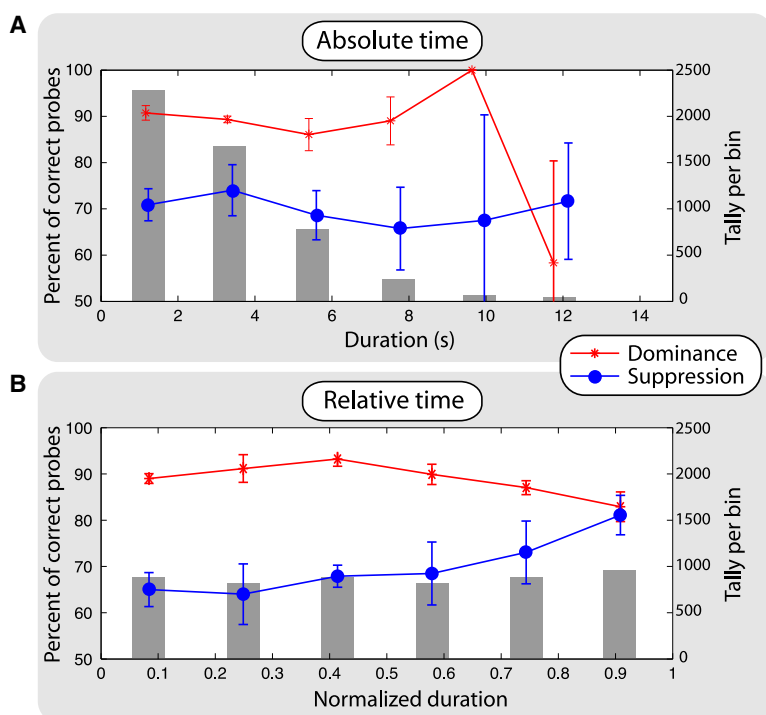


Figure 4. Results from Experiment 2

(A) The data points and lines show group means with standard error of those means for probe-detection performance (left y axis) for each rivalry state as a function of time after onset of that state (advanced by 450 ms to correct for observers' latency in responding to perceptual changes, although any value from 400 to 650 ms produces similar results), plotted on the x axis. We sorted times into six equal-width bins for dominance and for suppression (the range of times for dominance was slightly smaller than that for suppression). The gray bars show the number of observations in each time bin (right y axis) summed over dominance and suppression, with all observers pooled. Performance is better for dominance (red) than for suppression (blue), and there is no clear change in relative performance as a function of time. The gray bars show the typical gamma-shaped distribution of dominance times, explaining why probe performance data become so noisy in the last two time bins: there are very few observations in them.

(B) The data from (A) recoded as relative time by normalizing to the maximum time of each episode of rivalry. Normalizing the state durations equalizes the number of probes in each bin and reveals a clear change in relative performance over time. In the later time bins, dominance performance drops and suppression performance increases, consistent with the effects of adaption on reciprocal inhibition.

a rivalry phase. For the first time, this is consistent with the expected role of adaptation in the reciprocal inhibition model of rivalry. This adds binocular rivalry to the phenomena that the reciprocal inhibition theory can explain, including linked reflexes in movement [4, 35], control of eye movements [36], and interactions between vision and balance [37], suggesting that reciprocal inhibition is a general mechanism in the nervous system that can be exploited in diverse contexts.

Experimental Procedures

Observers

Six males, with ages ranging from 32 to 63, participated in experiment 1 after giving informed consent. Two observers were naive about the hypothesis being tested, and the other four were the authors of this paper. All have normal or corrected-to-normal vision and excellent stereopsis. Four of the six were tested at Vanderbilt University, and the other two were tested at the University of Sydney, along with one of the observers who was previously tested at Vanderbilt (R.B.). In experiment 2, observers were three of the authors and one female who was naive about the hypothesis. Experiments were approved by the ethics boards of the respective institutions.

Apparatus and Stimuli

Stimuli were created using Matlab with the Psychophysics Toolbox extensions [38, 39] running on a Macintosh computer. For test sessions administered at Vanderbilt University, stimuli were presented on a calibrated Mitsubishi color cathode ray tube (CRT) monitor (Diamond Pro 2020u; 1024 × 768 pixels, 100 Hz), the mean luminance of which was 31 cd/m². For test sessions administered at Sydney University, stimuli were presented on a LaCie color CRT monitor (Electron Blue 22" series 3; 1024 × 768 pixels, 100 Hz), the mean luminance of which was 27 cd/m².

At both testing locations, the two rival stimuli (Figure 1A) were a horizontal Gabor patch, presented to the observer's dominant eye, and a radial checkerboard pattern, presented to the nondominant eye (eye dominance was estimated based on relative predominance derived in pilot tracking sessions that employed equal-contrast rival targets). The Gabor patch had a circular Gaussian envelope with a standard deviation of 0.43°, and contained within this 1.8° circular patch was a horizontal sine wave grating whose spatial frequency was 2.5 cpd. The radial checkerboard was centered within a square region that was 1.8° per side and had 16 wedges and 6 bands radially, with sharp transitions between light and dark regions. These rival stimuli were presented simultaneously on the left and right halves of the monitor, with a center-to-center separation of 13.3°. Surrounding each rival stimulus was a square frame (0.4° in width) comprising black and white checks (see Figure 1A). These checks were binocularly matched and therefore provided dioptic stimuli for maintaining stable binocular alignment. These stimuli were viewed, one to each eye, through a stereoscope comprising four front-surface mirrors, giving an optical distance from the monitor to the eye of 82 cm. The entire apparatus was housed in a darkened test chamber. Observers gave their responses by pressing keys on the computer's keyboard.

For both testing locations, a bit-stealing technique was used to achieve an effective resolution of 10 bits on our gamma-corrected CRT monitors. The contrast of the Gabor (governed by the amplitude of the Gaussian window over the sinusoid) and the radial checkerboard were determined by pilot experiments that measured the alternation dynamics between the two stimuli. These experiments involved varying the relative contrasts of the stimuli to find low contrasts that would slow the rivalry process to a median duration of at least 3 s (allowing easier probing of a given rivalry phase) and that would produce equal predominance of each stimulus. In practice, this meant a mean stimulus contrast on the order of 25%.

Brief test probes were delivered to the eye viewing the Gabor patch to permit measurement of visual sensitivity during dominance and suppression phases. A test probe consisted of a contrast increment added to either the top or bottom half of the horizontal grating (Figure 1B). The sinusoid within the Gabor had a zero crossing that horizontally bisected the stimulus into equal upper and lower regions, allowing the contrast increment to be applied uniformly over each region. A temporal Gaussian profile was used to ramp the probe's contrast smoothly up and down to help reduce transients that can break rivalry suppression [40]. The standard deviation of the temporal Gaussian was 34 ms and was truncated at ±3 standard deviations (±100 ms).

Procedure

Experiment 1 comprised two phases: (1) the measurement of each observer's dominance duration distributions for the Gabor and radial checkerboard so that the median duration could be determined, and (2) the measurement of contrast increment thresholds for the Gabor test probes.

For the measurement of dominance durations, we required observers to track the rivalry between the Gabor and the radial checkerboard for at least five consecutive 60 s periods, using one computer key to indicate when the Gabor was completely dominant, another key when it was completely suppressed, and neither key when a piecemeal mixture of both was visible. From the resulting tracking records, we computed the median durations for dominance and suppression for the Gabor patch and used those values as the late probe delays for the probe detection portion of the experiment.

For the measurement of contrast increment thresholds for the Gabor test probes, we used two delays for presenting probes: an early condition, 200 ms after an observer's key press indicated that a stable dominance or suppression phase had been achieved (Figure 1C), and a late condition, when an observer's median suppression duration had elapsed after the key press. We varied the magnitude of the brief contrast increment applied to the top or bottom half of the Gabor using a staircase procedure driven by performance on a two-alternative forced-choice (2AFC) task. Over trials, the region of the Gabor patch receiving the increment was varied randomly, and the observer's task was to report using key presses whether the contrast increment appeared in the top or the bottom half of the grating (with error feedback provided). Each trial began with the appearance of the rival targets, and the observer waited for at least one complete cycle of rivalry before pressing and holding the space bar to signal the onset of the rivalry state being tested, either dominance (grating completely visible) or suppression (radial checkerboard completely visible).

Observers were instructed never to press the space bar during the transitory phases between dominance and suppression. Observers were instructed to release the space bar if the designated rival state changed before the probe appeared, aborting the trial. This latter instruction meant, therefore, that approximately half of trials were aborted during the late-probe conditions, because approximately 50% of rivalry phase durations were shorter than the median state. Those trials had no influence on the staircase procedure used to vary the probe contrast increment; we kept a tally of the number of aborted trials.

For testing performed at Vanderbilt University, the contrast increment was initially set to 50% of the contrast of the Gabor. Three consecutive correct responses on the 2AFC task reduced the contrast increment for the next trial by 30% of the current trial. A single incorrect response set the contrast increment for the next trial 30% higher. After four reversals, the contrast adjustment was reduced to 15%. When the number of reversals reached 12, the staircase was terminated and the contrast increment threshold for that staircase was defined as the average contrast increment value associated with the last six staircase reversals. For testing at the University of Sydney, contrast was varied over trials using the adaptive QUEST procedure, with six QUEST staircases each for early- and late-probe conditions administered during dominance and during suppression; their means were averaged into a final threshold estimate.

Experiment 2 also comprised two phases: (1) the measurement of each observer's thresholds under dominance and suppression, so as to choose a suitable contrast increment for the second phase, and (2) the measurement of forced-choice detection of probe location while observers were continually reporting their experiences of rivalry.

Supplemental Information

Supplemental Information includes Supplemental Discussion, Supplemental Results, Supplemental Experimental Procedures, three figures, and one table and can be found with this article online at [doi:10.1016/j.cub.2010.06.015](https://doi.org/10.1016/j.cub.2010.06.015).

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